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Parasites as biological tags of divergence of black-striped pipefish, *Syngnathus abaster* (Actinopterygii: Syngnathiformes: Syngnathidae), populations in their natural and acquired range

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Abstract

The presently reported study was intended to describe the current range of an Atlanto–Mediterranean fish, the black-striped pipefish, *Syngnathus abaster* Risso, 1827, in Ukrainian waters and to analyze biological tags (size parameters and parasites) of its different populations. The parasitological survey was carried at five different localities, including one marine site, two deltaic zones, and two localities in the middle Dnipro basin. The study provides comprehensive new data on parasites of the black-striped pipefish in Ukraine, with supporting data on its newly acquired freshwater range. A total of 21 parasite species (taxa) were revealed. Several parasite species were recorded for the first time on this host, i.e., *Trichodinella epizootica* (Raabe, 1950); *Trypanosoma* sp.; *Bothriocephalus scorpii* (Müller, 1776); *Progrillotia dasyatidis* Beveridge, Neifar et Euzet, 2004; *Ophiotaenia europaea* Odening, 1963; *Cryptocotyle jejuna* (Nicoll, 1907); *Metorchis xanthosomus* (Creplin, 1846); *Tylodelphys clavata* (von Nordmann, 1832); *Holostephanus luehei* Szidat, 1936; *Contracaecum rudolphii* Hartwich, 1964; *Mothocya epimerica* Costa in Hope, 1851; and Unionidae gen. sp. Formation of the species' parasite component community depends entirely on environmental factors, with local parasite community features forming due to 1) presence of "marine" unicellular parasite species (ciliates) in marine localities (10‰–17‰ salinity) only, the community forming as a refraction of relative stenohalinity (*Trichodina rectuncinata* Raabe, 1958), findings of "marine" ciliate species in freshwater locations representing examples of successful osmoconformation (*Trichodina partidisci* Lom, 1962); or 2) presence of multicellular parasites in localities with abiotic/biotic conditions that allow completion of complex life cycles, such as those of trematodes (freshwater/marine mollusks as obligate first hosts) or cestodes (freshwater/marine invertebrates as intermediate hosts or marine/freshwater vertebrates as definitive hosts).

Keywords

brackish water, freshwater, Mediterranean species, neolimnetics, range extension, Ukraine

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Introduction

Species range extension is a natural process stretched over time and it ultimately contributes to the formation of biodiversity (Alexandrov et al. 2007; Polačik et al. 2008). However, over recent decades, human activity has caused natural range borders to change significantly, spreading many species, including fishes (Bij de Vaate et al. 2002; García-Berthou et al. 2005; Hirsch et al. 2016). As a result, non-native (or alien) species are now having adverse effects (e.g., Ponto–Caspian gobiids in the Rhine River basin and the North-American Great Lakes, rainbow trout in European mountain locations, etc.) in many recipient ecosystems and, as such, they represent one of the biggest challenges for global biodiversity today (Leppäkoski et al. 2002; Hirsch et al. 2016).

Ukraine is located at a major crossing of transport corridors (land, freshwater, and marine), representing important routes for the spread of alien aquatic species (Alexandrov et al. 2007; Semenchenko et al. 2016). At least two crucial aquatic biological invasion routes pass through Ukraine's aquatic ecosystems, the so-called Southern and Central Corridors (Panov et al. 2009), and many Ponto–Caspian and Mediterranean species have now increased their ranges along these corridors (Tutman et al. 2012; Semenchenko et al. 2016; Marenkov 2018; Dobrzycka-Krahel et al. 2023). One such group is the "neolimnetics", which have a marine/brackish water origin but have spread into freshwater habitats in Ukraine and other European countries. These include species such as the Ponto–Caspian gobiids, the Ukrainian stickleback, *Pungitius platygaster* (Kessler, 1859); the black-striped pipefish, *Syngnathus abaster* Risso, 1827; and the big-scale sand smelt, *Atherina boyeri* Risso, 1810 (see Kvach and Kutsokon 2017).

The black-striped pipefish is an Atlanto–Mediterranean fish species with a natural range from the southern Gulf of Biscay in the north to Gibraltar in the south, the Mediterranean and Black Seas, and the estuarine zones of their rivers (Dawson 1986). It has a maximum body length of 21.5 cm (more commonly 16.0 cm) and a maximum weight of 3.0 g (age unknown). It lives along the coastal zone, mainly in shallow waters, and is tolerant of waters with different salinities (e.g., it is found along the coast of Crimea and in the Dnipro River near Kyiv), though it is far more common and numerous in estuaries and desalinated coasts than in open sea areas. The species matures at 2–3 years of age with a body length of ca. 7.0 cm and spawns from April to September, laying up to 200 eggs (usually ca. 100). The male accepts eggs from several females and carries them around in a brood sac. The species feeds on plankton and benthic organisms, tiny and medium-sized crustaceans, insect larvae, fish roe, and occasionally algae.

While the species has a brackish water origin, its high tolerance to freshwater has allowed it to spread up all large rivers in the Black Sea basin, i.e., the Danube, Dniester, Southern Buh, and Dnipro (Slastenenko 1956). It has been recorded in the Ros River (Dnipro basin) since the beginning of the 20th century and is now present in all reservoirs and the rivers Prypyat and Desna, though it is presently only found in small tributaries in the lower part of the basin (Beling 1923; Zimbalevskaya et al. 1989; Movchan 2012; Movchan and Roman 2014). In the Danube, the species has been recorded as far as Serbia and Bosnia and Herzegovina (Sekulić et al. 1999; Tutman et al. 2012).

Parasites are commonly used as biological tags of their host populations (Moser 1991; Mackenzie 2002). Fish parasite communities can be used to discriminate fish stocks and populations and, as such, a process known as "biological tagging" (Catalano et al. 2014; Poulin and Kamiya 2015; Kvach et al. 2017; Kutsokon et al. 2022) and the same biological tag can be used as a marker to clarify the possible origin of invasive populations (Hohenadler et al. 2018a, 2018b; Ondračková et al. 2012b; 2019; 2021). A total of 18 parasite species have been recorded for populations of the Black Sea basin black-striped pipefish (Gaevskaya et al. 1975). However, data for parasites in its acquired range are primarily related to the Danubian population in Bulgaria, where nine species were recorded (Ondračková et al. 2012a), and the Dnipro population in Ukraine, where just two ciliate species were recorded (*Trichodina partidisci* Lom, 1962 and *Trichodina acuta* Lom, 1961; see Yurishinets 2010). Consequently, very little is known about parasites acquired in the species' non-native freshwater habitats.

Therefore, the presently reported study aimed to describe the current range of black-striped pipefish in Ukrainian waters and obtain biological tag data (parasites) for the populations.

Materials and methods

The fish were sampled using the 10 × 1 m dipnet and a 1 × 0.5 m diameter hand net (0.5 cm mesh). In total, 107 fish were sampled from five different localities during the warm seasons of 2020–2021 (Table 1; Fig. 1). These included one marine locality (Gulf of Odesa), two deltaic zones (Danube and Dniester deltas), and two localities in the middle Dnipro basin (Lake Vyazky and the Stuhna River). In the Danube Delta, fish were sampled from three different sites (Fig. 1), considered the same locali-

Table 1. Number (*n*) and standard length (SL) of *Syngnathus abaster* from different localities in Ukraine.

Locality		Geographic coordinates	*n*	Standard length	
				Mean ± SD	Min–max
Black Sea (Gulf of Odesa)		46.443020; 30.772734	37	114.9 ± 22.8	65–203
Danube Delta		45.408702; 29.583393	20	107.5 ± 18.3	78–145
Dniester Delta		46.466634; 30.197059	17	104.1 ± 29.0	58–166
Dnipro basin	Lake Vyazky	50.368624; 30.653934	15	111.5 ± 16.2	79–140
	Stuhna River	50.149168; 30.731980	16	102.9 ± 24.0	51–143

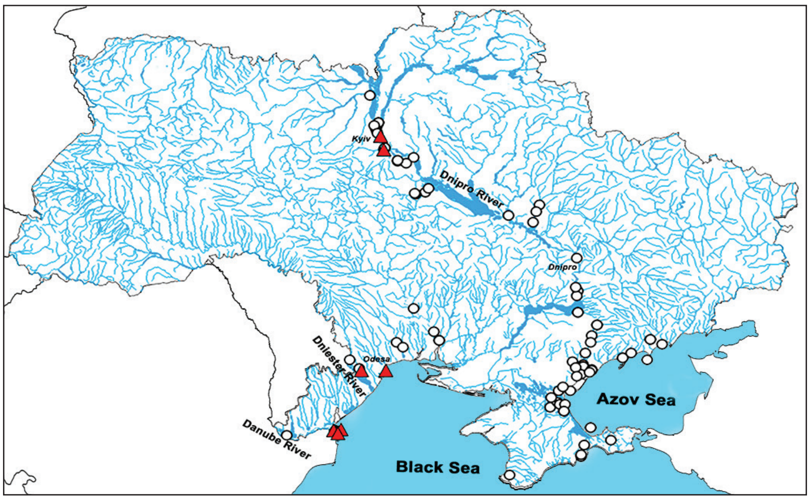

Figure 1. Map of Ukraine indicating the sampling localities with current sampling sites (2020–2021) marked with triangles.

ty for further analysis. The salinity of the Gulf of Odesa is 10‰–17‰ depending on the season (Zaitsev 1992). Once caught, the fish were transported alive to the laboratory in aerated cans filled with water from the sampling site, where they were placed in aerated aquaria containing water from the place of capture for no more than two days (Kvach et al. 2016) before being examined for parasites.

Findings of black-striped pipefish from other sites were registered (without removing the fish) and used to evaluate the range of the species (Fig. 1). In addition, a literature search was undertaken (Movchan 2012; Movchan and Roman 2014; Demchenko 2017; Kutsokon and Kvach 2021; Kutsokon and Roman 2021; Kutsokon et al. 2021a, 2021b) to obtain the latest information on the species' present-day range.

Prior to dissection, the standard length (SL, mm) and sex was determined for each fish (Table 1). After humanely sacrificing the fish, smears of gill and fins mucosa were taken, dried, and stained according to Klein (1958) to identify ciliates. Likewise, blood smears were dried and stained in hematoxylin (Giemsa 1904) to identify other unicellular organisms. Fresh smears from muscle and the gall and uterine bladders were examined for myxozoans and any living spores mounted onto gelatin gel as semi-permanent preparations for further identification. Monogeneans were placed onto glass slides and mounted in glycerin-ammonium-picrate for morphological study (Malmberg 1957). Cestodes, digeneans, and nematodes were fixed with hot 4% formalin (Cribb and Bray 2010), and glochidia and crustaceans in cold 4% formalin. Acanthocephalans and nematodes were mounted in glycerin as temporary slides for further species identification, while cestodes and digeneans were stained in iron acetocarmine and mounted onto Canada balsam slides (Georgiev et al. 1986). All parasites were identified to the lowest possible taxa, with parasite taxonomy presented following the World Register of Marine Species (WoRMS 2022). Parasitological terminology and principal indices, such as prevalence, intensity, mean intensity, and abundance, were used in accordance with Bush et al. (1997):

Prevalence (P)

$$P = \frac{n}{N} \times 100\%$$

where n is the number of infected fish and N is the number of fish examined.

Intensity (of infection) (I) is the number of individuals of a particular parasite species in a single infected host (individual fish) usually presented as the intensity range (I_R) (minimum–maximum).

Mean intensity (of infection) (I_M)

$$I_M = \frac{N_{TP}}{N_{inf}}$$

where N_{TP} is the total number of individuals of a particular parasite species found in all fish examined and N_{inf} is the number of infected fish.

Abundance (A)

$$A = \frac{N_T}{N}$$

where N_T is the total number of individuals of a particular parasite species found in all fish examined and N is the number of fish examined.

For microparasites (unicellular and myxozoans), only the prevalence was calculated, with the intensity of infection evaluated by the presence of microparasites in the microscope's field of view (Mierzejewska et al. 2012) as:

- Sporadic (S), from 1 to < 10 individuals in the material examined;
- Not numerous (NN), < 10 individuals in < 10% of field of view;
- Numerous (N), up to 20 individuals in > 50% of field of view;
- Very numerous (VN), > 20 individuals in > 50% of field of view;
- Mass (M), dozens of individuals in each field of view.

The Czekanowski–Sørensen index (CSI) was calculated (Sørensen 1948) to analyze differences in parasite fauna at different localities, with differences considered high in cases where index parameters were < 50%.

Statistical differences in length were evaluated using *t*-tests and *F*-tests for comparing two samples in Statistica for Windows 10 (StatSoft). Standard deviation values (SD) were calculated for mean parameters in each case. Visualization of fish size data was carried out in PAST v.4.03 (Paleontological Statistics Software system), using the search statistics methods (box and whisker), comparative analysis, and cluster analysis (Hammer et al. 2001). Discriminant analysis was then performed to evaluate differences in the respective parasite communities.

Results

We observed no significant difference in the length of black-striped pipefish from marine (Gulf of Odesa), estuarine (Danube and Dniester deltas), or freshwater (Lake Vyazky and Stuhna River) localities (Fig. 2).

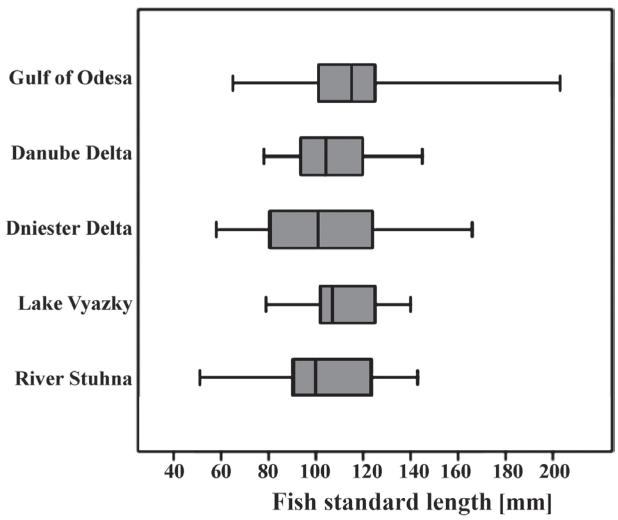

Figure 2. Box (median, 50% sample size) and whisker (min, max) plot for size (SL, mm) of *Syngnathus abaster* populations from different localities in Ukraine.

Based on published literature and databases, we consider the modern range of black-striped pipefish in Ukraine to include both brackish and freshwaters of the Black Sea basin (Fig. 1). In rivers where the populations have been established since the middle of the 20th century, the species is still to be found mainly in the lower reaches, though it has spread as far as the Belarus border in the Dnipro Reservoir cascade (Fig. 1), and into many of the lower first-order tributaries of the Dnipro River, regardless of size (i.e., medium rivers such as the Ros and Desna, and small rivers such as the Leglych and Mokra Moskovka). Despite much long-term research in the area, the black-striped pipefish has not been found in upper-flow tributaries to date. While the highest recorded finding was in the middle flow of the Ros River in 1923 (Beling 1923), all later records of the species have been from the lower reaches of the river (Kutsokon 2010). The species is also found in the lower reaches of the Dniester, Danube (along the entire stretch within the borders of Ukraine), Tyligul, Southern Buh, and rivers of the Crimean and Northern Azov coasts (Demchenko 2017; Kutsokon and Kvach 2021; Kutsokon and Roman 2021; Kutsokon et al. 2021b).

The parasite fauna of Ukrainian black-striped pipefish consisted of 21 parasite species (taxa), including five unicellular taxa, four cestodes, nine digeneans, one nematode, one isopod, and unidentified glochidia: *Trichodina* spp., *Trichodina partidisci* Lom, 1962, *Trichodina rectuncinata* Raabe, 1958, *Trichodinella epizootica* (Raabe, 1950) [CILIOPHORA]; *Trypanosoma* sp. [KINETOPLASTEA]; *Proteocephalus* sp., *Bothriocephalus scorpii* (Müller, 1776), *Progrillotia dasyatidis* Beveridge, Neifar et Euzet, 2004, *Ophiotaenia europaea* Odening, 1963 [CESTODA]; *Orientocreadium pseudobagri* Yamaguti, 1934, *Nicolla skrjabini* (Iwanitzky, 1928), *Cryptocotyle concava* (Creplin, 1825), *Cryptocotyle jejuna* (Nicoll, 1907), *Timoniella imbutiformis* (Molin, 1859), *Metorchis xanthosomus* (Creplin, 1846), *Diplostomum* spp., *Tylodelphys clavata* (von Nordmann, 1832), *Holostephanus luehei* Szidat, 1936 [DIGENEA]; *Contracaecum rudolphii* Hartwich, 1964 [NEMATODA]; *Mothocya epimerica* Costa in Hope, 1851 [CRUSTACEA]; Unionidae gen. sp. [BIVALVIA] (Table 2). Parasite richness varied from 2–3 species in the Dnipro basin and up to eight species in the Black Sea. The majority of parasites were represented by larval stages, with just two digeneans—*Orientocreadium pseudobagri*, *Nicolla skrjabini*—and an isopod *Mothocya epimerica* found as adults.

The most numerous species were ciliates of *Trichodina* spp., with the prevalence varying from 5.9% to 100% and intensity of infection of up to several thousand cells (Table 2). Among the ciliates, we identified at least three species, most represented by *Trichodina partidisci*, found in both freshwater (except the isolated Lake Vyazky) and marine/brackish sites. This is a small-sized species (23.7–31.5 µm; 27.6 ± 2.9), with a denticle ring diameter of 10.4–16.1 µm (13.5 ± 2.0) and a denticle number of 18–24 (22). It can be recognized by the broadly rounded distal surface of its denticle blade and the (usually) few, irregular unstained granules in the central part of its adhesive disc (Fig. 3). *Trichodina rectuncinata*, a species common on marine fish, was only found in the Gulf of Odesa. Again, this is a small-sized species (23.0–30.5 µm, 28.8 ± 1.7) with a denticle ring diameter of 12.3–15.2 µm (13.6 ± 1.2) and a denticle number of 22–25 (24), recognized by a triangular blade with a cavity in the center (Fig. 3). *Trichodinella epizootica*, a small mobilid typical of freshwaters, was registered in just one fish from the Danube Delta.

Ukrainian pipefish populations differed with the abundance values for *Nicolla skrjabini* and *Diplostomum* spp.

Table 2. Parasite communities of *Syngnathus abaster* from various localities in Ukraine (as determined in the presently reported study).

Parasite species Developmental stage Location on host	Index	Black Sea (Gulf of Odesa)	Danube Delta	Dniester Delta	Dnipro basin	
					Lake Vyazky	Stuhna River
Trichodina spp. [*Trichodina partidisci* Lom, 1962,	P [%]	64.1	68.2	5.9		22.2
Trichodina rectuncinata Raabe, 1958, *Trichodina* sp.,	I_R	S–M	S–M	NN		VN
Trichodinella epizootica (Raabe, 1950)]						
trophont						
gills, skin, fins						
Trypanosoma sp.	P [%]			5.9		
trypomastigote	I_R			NN		
blood						
Proteocephalus sp.	P [%]		4.5			
plerocercoid	$I_M \pm SD$		1.0			
gut	I_R		1			
	A		0.05			
Bothriocephalus scorpii	P [%]	7.7				
plerocercoid	$I_M \pm SD$	2.7 ± 2.1				
gut	I_R	1–5				
	A	0.5				
Progrillotia dasyatidis	P [%]	5.1				
plerocercoid	$I_M \pm SD$	4.5 ± 0.7				
gut	I_R	4–5				
	A	0.5				
Ophiotaenia europaea	P [%]			5.9		
plerocercoid	$I_M \pm SD$			1.0		
mesentery	I_R			1		
	A			0.1		
Orientocreadium pseudobagri	P [%]		13.6	5.9		
marita	$I_M \pm SD$		5.3 ± 5.9	1.0		
gut	I_R		1–12	1		
	A		0.7	0.1		
Nicolla skrjabini	P [%]			11.8		
marita	$I_M \pm SD$			1.5 ± 0.7		
gut	I_R			1–2		
	A			0.2		
Cryptocotyle concava	P [%]	10.3				
metacercariae	$I_M \pm SD$	4.5 ± 3.9				
mesentery, fins	I_R	1–10				
	A	1.1				
Cryptocotyle jejuna	P [%]	7.7				
metacercariae	$I_M \pm SD$	4.7 ± 4.7				
mesentery, fins	I_R	1–10				
	A	0.8				
Timoniella imbutiformis	P [%]	2.6				
metacercariae	$I_M \pm SD$	1.0				
muscles	I_R	1				
	A	0.1				
Metorchis xanthosomus	P [%]		4.5			
metacercariae	$I_M \pm SD$		1.0			
mesentery	I_R		1			
	A		0.05			
Diplostomum spp.	P [%]				26.7	16.7
metacercariae	$I_M \pm SD$				1.25 ± 0.5	1.3 ± 0.6
eyes	I_R				1–2	1–2
	A				0.3	0.2
Tylodelphys clavata	P [%]			5.9		
metacercariae	$I_M \pm SD$			1.0		
eyes	I_R			1		
	A			0.1		
Holostephanus luehei	P [%]		9.1			
metacercariae	$I_M \pm SD$		1.0			
mesentery	I_R		1			
	A		0.1			

Parasite species Developmental stage Location on host	Index	Black Sea (Gulf of Odesa)	Danube Delta	Dniester Delta	Dnipro basin	
					Lake Vyazky	Stuhna River
Contracaecum rudolphii	*P* [%]	2.6	4.5			
larvae	$I_M \pm$ SD	4.0	2			
mesentery	I_R	4	2			
	A	0.2	0.1			
Mothocya epimerica	*P* [%]	2.6				
adult	$I_M \pm$ SD	1.0				
gills	I_R	1				
	A	0.1				
Unionidae gen. sp.	*P* [%]			5.9	6.7	5.6
glochidia	$I_M \pm$ SD			5.0	2	5
gills	I_R			5	2	5
	A			0.3	0.1	0.3

P = prevalence, I_M = mean intensity, I_R = intensity range (min–max); *A* = abundance; SD = standard deviation; values of microparasites intensity (range) according to Mierzejewska et al. (2012) as: S = sporadic, NN = not numerous, N = numerous, VN = very numerous, M = mass.

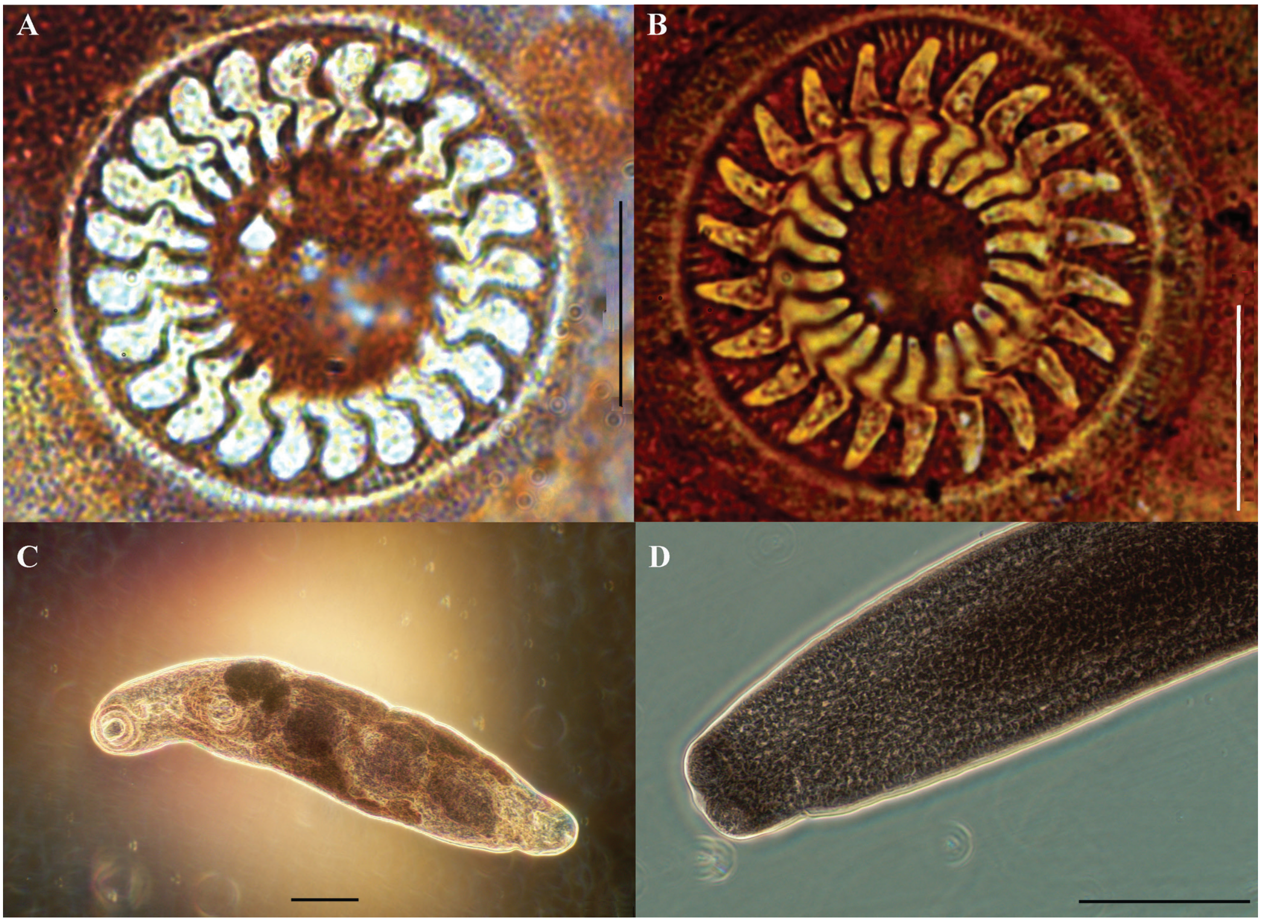

Figure 3. Typical parasites of *Syngnathus abaster* from different localities in Ukraine. **A**) *Trichodina partidisci* (Danube Delta); **B**) *Trichodina rectuncinata* (Black Sea, Gulf of Odesa); **C**) *Orientocreadium pseudobagri* (Danube Delta); **D**) *Proteocephalus* sp. (Danube Delta). Scale bars: 10 µm (A, B), 300 µm (C, D).

(Table 3), with a comparative analysis of parasite communities using the Czekanowski–Sørensen index (CSI) distinguished marine populations from freshwater/brackish populations (Fig. 4). CSI, Mahalanobis distance, and the Fischer criterium all showed significant differences between the Gulf of Odesa and the Danube and Dniester deltas (Table 4), with CSI parameters showing the largest differences between all localities.

Discussion

This study provides comprehensive new data on the parasites of black-striped pipefish in Ukraine, along with supporting data on its acquired range in Ukrainian freshwaters. Our new data confirm that the species is now found in the coastal zones of the Black Sea and the Sea of Azov and the deltaic zones of rivers and reservoirs of

Table 3. Discriminant function analysis of parasite communities of *Syngnathus abaster* from different localities in Ukraine.

Parasite species	Wilks' Lambda	Partial Lambda	*F*-remove (4,89)	*P*-value	Toler.	1-Toler. (R^2)
Trichodina spp.	0.42	0.91	2.08	0.09	0.59	0.41
Trypanosoma sp.	0.41	0.93	1.60	0.18	0.98	0.02
Bothriocephalus scorpii	0.41	0.95	1.15	0.34	0.98	0.02
Ophiotaenia europaea	0.41	0.93	1.60	0.18	0.98	0.02
Proteocephalus sp.	0.40	0.95	1.06	0.38	0.99	0.01
Progrillotia dasyatidis	0.39	1.00	0.02	1.00	0.54	0.46
Nicolla skrjabini	**0.44**	**0.89**	**2.86**	**0.03**	**0.97**	**0.03**
Orientocreadium pseudobagri	0.42	0.91	2.16	0.08	0.06	0.94
Cryptocotyle concavum	0.39	1.00	0.10	0.98	0.03	0.97
Cryptocotyle jejuna	0.39	1.00	0.03	1.00	0.03	0.97
Timoniella imbutiformis	0.39	0.98	0.45	0.77	0.99	0.01
Diplostomum spp.	**0.45**	**0.87**	**3.39**	**0.01**	**0.98**	**0.02**
Tylodelphys clavata	0.41	0.93	1.60	0.18	0.98	0.02
Holostephanus luehei	0.42	0.92	1.98	0.11	0.84	0.16
Metorchis xanthosomum	0.41	0.94	1.31	0.27	0.06	0.94
Contracaecum rudolphii	0.39	0.99	0.28	0.89	0.54	0.46
Mothocya epimerica	0.39	1.00	0.01	1.00	0.25	0.75
Unionidae gen. sp.	0.40	0.96	0.89	0.48	0.92	0.08

Wilks' Lambda: approx. 0.38655; *F* (72.352) = 1.3380; $P < 0.05$); **Bold** font dentotes significant differences.

Table 4. Matrix of differences between parasite fauna/communities of pipefish from different localities.

Locality	Index	Black Sea (Gulf of Odesa)	Danube Delta	Dniester Delta	Lake Vyazky
Danube Delta	ICS	**28.57**	100.00		
	MD	**2.72**	0.00		
	F	**1.78**			
Dniester Delta	ICS	**13.33**	**30.77**	100.00	
	MD	**4.21**	**4.27**	0.00	
	F	**2.33**	**1.91**		
Lake Vyazky	ICS	**0.00**	**0.00**	**22.22**	100.00
	MD	2.42	2.78	3.92	0.00
	F	1.22	1.16	1.46	
Stuhna River	ICS	**18.18**	**22.22**	**40.00**	**40.00**
	MD	1.72	2.31	3.12	0.21
	F	0.99	1.07	1.27	0.08

CSI = Czekanowski–Sørensen index, MD = squared Mahalanobis distances, F = Fischer criterium. Significant differences ($P < 0.05$) are marked in **bold.**

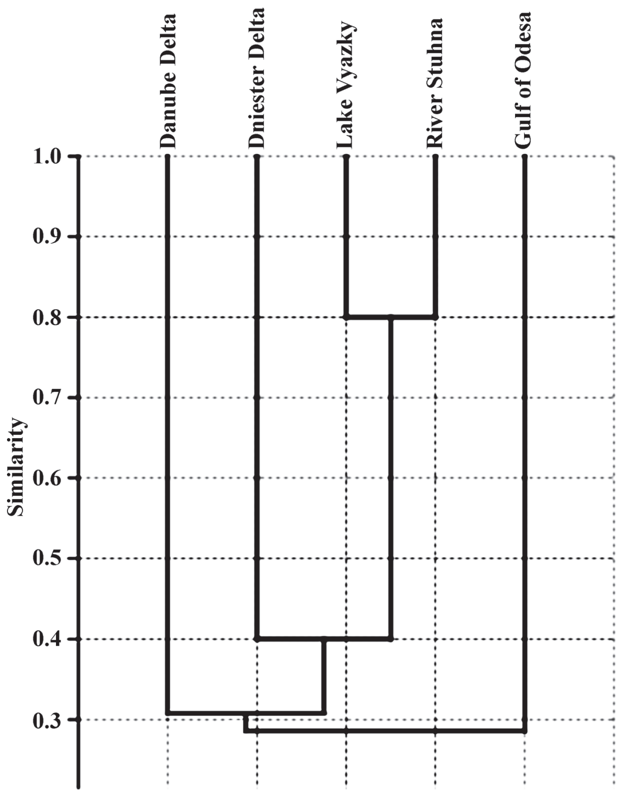

Figure 4. Dendrogram of similarity expressed by Czekanowski–Sørensen index for parasites component communities of *Syngnathus abaster* at different localities in Ukraine.

the Dnipro basin (Movchan 2011; Snigirov et al. 2020). However, the only new findings we recorded were inside the species' established range in the Lower Dnipro basin, suggesting that its Ukrainian range has probably now stabilized since it started spreading in the middle of the 20th century.

Several parasite species were registered on this host for the first time, i.e., *Trichodinella epizootica*, *Trypanosoma* sp., *Bothriocephalus scorpii*, *Progrillotia dasyatidis*, *Ophiotaenia europaea*, *Cryptocotyle jejuna*, *Metorchis xanthosomus*, *Tylodelphys clavata*, *Holostephanus luehei*, *Contracaecum rudolphii*, *Mothocya epimerica*; and Unionidae gen. sp. (Table 2). In addition, we confirmed the presence of several species previously recorded on the black-striped pipefish, including several ciliate species. While these are common on a wide spectrum of freshwater and brackish water hosts (Kostenko 1981; Grupcheva et al. 1989; Yurishinets 2010), no specific ciliates were previously known for black-striped pipefish. The most common species found was *Trichodina partidisci*, a parasite of mugilid fish in the Black Sea (Lom 1962) that has a wide spectrum of hosts (Grupcheva et al. 1989; Lom and Dyková 1992). In Ukrainian freshwaters, it is known from pipefish in the middle Dnieper basin (Yurishinets 2010). A second species, *Trichodina rectuncinata*, a widespread marine fish parasite, has previously been recorded in different areas of the Atlantic and Pacific oceans (Xu et al. 2001; Islas-Ortega et al. 2020; Öztürk and Güven 2022).

All four cestode species on black-striped pipefish were only registered at the plerocercoid stage. Two of the cestodes, *Bothriocephalus scorpii* and *Progrillotia dasyatidis* were marine species reported in the Gulf of Odesa. *Bothriocephalus scorpii* has been known as a parasite of turbot, *Scophthalmus maximus* (Linnaeus, 1758), scorpionfish (Scorpaenidae), mullet (Mugilidae), mackerel (Scombridae), and rays (Batoidea); *Progrillotia dasyatidis* is a parasite of a stingray, *Dasyatis pastinaca* (Linnaeus, 1758) (see Beveridge et al. 2004; Kuchta et al. 2008). While *Progrillotia dasyatidis* is common in fishes from the Gulf of Odesa (Kvach et al. 2022), *Bothriocephalus scorpii* has only been registered in adjacent water bodies (Kvach 2010). *Proteocephalus* sp. (see Fig. 3b), recorded in pipefish from the Danube, is a common parasite of Danubian freshwater fishes (Bauer 1985) and has previously been reported in pipefish from the middle Danube (Ondračková et al. 2012a). Finally, *Ophiotaenia europaea* is a parasite of grass snakes that uses fishes as its paratenic hosts (Sharpilo and Monchenko 1971). While it has previously been registered in fish from the Danube Delta (Kvach et al. 2020), this is the first time it has been registered in the Dniester River.

While the freshwater digeneans, *Orientocreadium pseudobagri* and *Nicolla skrjabini*, were recorded as adults in the gut of pipefish from the Danube and Dniester deltas (Table 2; Fig. 3), other digeneans were only represented by metacercariae, with either marine fish as their definitive hosts (*Timoniella imbutiformis*) or fish-eating birds (*Cryptocotyle concava*, *Cryptocotyle jejuna*, *Metorchis xanthosomus*, *Diplostomum* sp., *Tylodelphys clavata*). Moreover, we have not recorded those metacercariae with a wide spectrum of hosts, e.g., Cyathocotylidae fam. spp., *Echinochasmus perfoliatus* (Ratz, 1908), and *Metagonimus* sp., despite these having previously been reported in pipefish from the middle Danube basin (Ondračková et al. 2012a).

In the Gulf of Odesa and the Danube Delta, sporadic cases of parasitism by *Contracaecum rudolphii* nematode larvae were noted, the adult worms being common parasites of pelicans, herons, mergansers, and cormorants (Sreedevi et al. 2017). Previous authors (e.g., Gaevskaya et al. 1975) have also noted the presence of another species of this genus, *Contracaecum microcephalum* (Rudolphi, 1809), along with larvae of *Agamonema* sp. nematode in the parasitefauna of marine pipefish.

The isopod *Mothocya epimerica*, a parasite of the branchial and oral cavities of sand-smelts (*Atherina* spp.), was only noted at a marine location with few indications of invasion (Bruce 1986; Leonardos and Trilles 2004). The parasitic copepods *Ergasilus lizae* Krøyer, 1863 and *Ergasilus ponticus* Markevich, 1940 have also previously been reported from marine populations of the black-striped pipefish (Gaevskaya et al. 1975).

Parasitism on the gills of unionid bivalve larvae (Unionidae) was noted for three of four freshwater localities, though with relatively low invasion rates (P = 5%–7%, I_R = 2–5 ind.).

The acanthocephalans *Paracanthocephaloides incrassatus* (Molin, 1858) (see Gaevskaya et al. 1975) and *Acanthocephaloides irregularis* Amin, Oğuz, Heckman, Tepe & Kvach, 2011 (see Amin et al. 2011) have both been recorded in pipefish populations from Black Sea localities, while the acquisition of *Pomphorhynchus laevis* (Zoega in Müller, 1776) has been confirmed from the middle Danube (Ondračková et al. 2012a). We have not found, however, the above-mentioned parasite species during the presently reported study.

The black-striped pipefish is now widespread in Ukrainian bodies of water, particularly in coastal brackish and freshwaters of the Black Sea and the Sea of Azov basins. In Ukraine, it is found along all shores of the Black and Azov Seas and in the estuaries, near-estuary and estuarine zones of their rivers, from where it has entered reservoirs and rivers connected to the sea (below the Danube, Dniester, and Southern Buh). It is also found in all reservoirs along the Dnipro and the Siversky Donets River (Movchan 2011). Previous studies have confirmed differences in biotope preferences between marine pipefish, which prefer plant thickets, and those in freshwaters, which prefer muddy biotopes (Ondračková et al. 2012a; middle Danube).

Ondračková et al. (2012a) noted the absence of any parasites specific to this fish species, suggesting that the formation of the species' parasite component communities depends entirely on the environmental factors affecting each population. In such cases, the local features of the parasite communities will depend on the following:

- The presence of "marine" species of unicellular parasites (ciliophores) in marine localities (10‰–17‰ salinity) only as a refraction of relative stenohalinity (*Trichodina rectuncinata*), or findings of "marine" ciliate species in freshwater locations, as an example of successful osmoconformation (*Trichodina partidisci*).
- The presence of multicellular parasites in localities with abiotic/biotic conditions that allow completion of complex life cycles, i.e., trematodes (freshwater/marine mollusks as obligate first hosts) or cestodes (freshwater/marine invertebrates as intermediate hosts or marine/freshwater vertebrates as definitive hosts).

Overall, the parasite fauna of neolimnetic black-striped pipefish exhibits two main parasite community formation strategies in their acquired ecosystems:

- Parasite release (very poor communities in freshwater).
- Acquisition of local parasite species, which have overcome the filters of encounter and adaptation (Combes 1995).

Our findings confirm that analyzing changes in the structure of neolimnetic fish parasitic communities that overcome geographical and ecological barriers is a convenient model for establishing the patterns and features of hydrobiont distribution beyond the boundaries of natural habitats.

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References

Alexandrov B, Boltachev A, Kharchenko T, Lyashenko A, Son M, Tsarenko P, Zhukinsky V (2007) Trends of aquatic alien species invasions in Ukraine. Aquatic Invasions 2(3): 215–242. https://doi.org/10.3391/ai.2007.2.3.8

Amin OM, Oğuz MC, Heckmann RA, Tepe Y, Kvach Y (2011) *Acanthocephaloides irregularis* n. sp. (Acanthocephala: Arhythmacanthidae) from marine fishes off the Ukrainian Black Sea coast. Systematic Parasitology 80(2): 125–135. https://doi.org/10.1007/s11230-011-9312-0

Bauer ON (1985) Opredelitel′ parazitov presnovodnyh ryb fauny SSSR, Tom 2, Parazitičeskie mnogokletočnye (Pervaâ čast′). Izdatel′stvo Nauka, Leningrad, USSR, 425 pp. [In Russian]

Beling DE (1923) Zametki po ihtiofaune Ukrainy. 1. Morskaâ igla – *Syngnathus nigrolineatus* Eischw. v bassejne Dnepra. Russkij gibrobiologičeskij žurnal 2(3–4): 71–73. [In Russian]

Beveridge I, Neifar L, Euzet L (2004) Review of the genus *Progrillotia* Dollfus, 1946 (Cestoda: Trypanorhyncha), with a redescription of *Progrillotia pastinacae* Dollfus, 1946 and description of *Progrillotia dasyatidis* sp. n. Folia Parasitologica 51(1): 33–44. https://doi.org/10.14411/fp.2004.005

Bij de Vaate A, Jażdżewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto–Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59(7): 1159–1174. https://doi.org/10.1139/f02-098

Bruce NL (1986) Revision of the isopod crustacean genus *Mothocya* Costa, in Hope, 1851 (Cymothoidae: Flabellifera), parasitic on marine fishes. Journal of Natural History 20(5): 1089–1192. https://doi.org/10.1080/00222938600770781

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83(4): 575–583. https://doi.org/10.2307/3284227

Catalano SR, Whittington ID, Donnellan SC, Gillanders BM (2014) Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances, and comments on a holistic approach. International Journal for Parasitology, Parasites and Wildlife 3(2): 220–226. https://doi.org/10.1016/j.ijppaw.2013.11.001

Combes C (1995) Interactions durables. Ecologie et évolution du parasitisme. Masson, coll. Ecologie, n° 26, Paris, France, 524 pp.

Cribb TH, Bray RA (2010) Gut wash, body soak, blender and heat-fixation: Approaches to the effective collection, fixation, and preservation of trematodes of fishes. Systematic Parasitology 76(1): 1–7. https://doi.org/10.1007/s11230-010-9229-z

Dawson CE (1986) Syngnathidae. Pp. 628–639. In: Whitehead PJP, Bauchot M-L, Hureau J-C, Nielsen J, Tortonese E (Eds) Fishes of the North-eastern Atlantic and the Mediterranean, Volume 2. UNESCO, Paris.

Demchenko V (2017) Fishes of Ukraine. Ukrainian Biodiversity Information Network. http://ukrbin.com/literature.php?sort=id&action=reltaxa&id=3978

Dobrzycka-Krahel A, Stepien CA, Nuc Z (2023) Growing neocosmopolitan distributions of invertebrate aquatic invasive species due to euryhaline geographic history and human-mediated dispersal: Origins from the Ponto–Caspian versus other regions. Ecological Processes 12: 2. https://doi.org/10.1186/s13717-022-00412-x

Gaevskaya AV, Gusev AV, Delyamure SL, Donets ZS, Iskova NI, Kornyushin VV, Kovaleva AA, Margaritov NM, Markevich AP, Mordvinova TN, Naidenova NN, Nikolaeva VM, Parukhin AM, Pogoreltseva TP, Smogorzhevskaya LA, Solonchenko AI, Shtein GA, Shulman SS (1975) Opredelitel′ parazitov pozvonočnyh Černogo i Azovskogo morej. Naukova Dumka, Kiev, USSR, 552 pp. [In Russian]

García-Berthou E, Alcaraz C, Pou-Rovira Q, Zamora L, Coenders G, Feo C (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 62(2): 453–463. https://doi.org/10.1139/f05-017

Georgiev B, Biserkov V, Genov T (1986) *In toto* staining method for cestodes with iron acetocarmine. Helminthologia 23: 279–281.

Giemsa G (1904) Eine Vereinfachung und Vervollkommnung meiner Methylenazur-Methylenblau-Eosin-Färbemethode zur Erzielungder Romanowsky-Nacht'schen Chromatin-Färbung. Centralblatt für Bakteriologie. Parasitenkunde und Infektionskrankheiten 37: 308–311.

Grupcheva G, Lom J, Dyková I (1989) Trichodinids (Ciliata: Urceolariidae) from gills of some marine fishes with the description of *Trichodina zaikai* sp. n. Folia Parasitologica 36(3): 193–207.

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 9.

Hirsch PE, N'Guyen A, Adrian-Kalchhauser I, Burkhardt-Holm P (2016) What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check. Ambio 45(3): 267–279. https://doi.org/10.1007/s13280-015-0718-9

Hohenadler MAA, Honka KI, Emde S, Klimpel S, Sures B (2018a) First evidence for a possible invasional meltdown among invasive fish parasites. Scientific Reports 8(1): 15085. https://doi.org/10.1038/s41598-018-33445-4

Hohenadler MAA, Nachev M, Thielen F, Taraschewski H, Grabner D, Sures B (2018b) *Pomphorhynchus laevis*: An invasive species in the river Rhine? Biological Invasions 20(1): 707–217. https://doi.org/10.1007/s10530-017-1527-9

Islas-Ortega AG, Basson L, Marcotegui P, Ruiz-Campos G, de Jager GP, Rivas G, Aguilar-Aguilar R (2020) Trichodinids (Ciliophora: Trichodinidae) on rocky-tidal fishes from the Baja California peninsula, Mexico. Journal of Parasitology 106(5): 689–698. https://doi.org/10.1645/20-80

Klein BM (1958) The dry silver method and its proper use. Journal of Protozoology 5(2): 99–103. https://doi.org/10.1111/j.1550-7408.1958.tb02535.x

Kostenko SM (1981) Fauna Ukraïny , tom 36, vypusk 4, Urtseoliariidy (peritrihi, mobîlîï). Naukova Dumka, Kyiv, URSR, 146 pp. [In Ukrainian]

Kuchta R, Scholz T, Bray RA (2008) Revision of the order Bothriocephalidea Kuchta, Scholz, Brabec et Bray, 2008 (Eucestoda) with amended generic diagnoses and keys to families and genera. Systematic Parasitology 71(2): 81–136. https://doi.org/10.1007/s11230-008-9153-7

Kutsokon YK (2010) Sučasnij vidovij sklad ribnoho naselennâ basejnu rîčki Ros'. Materîali mîžnarodnoï naukovoï konferencîï. Problemi vivčennâ î ohoroni tvarinnoho svîtu u prirodnih î antropogennih ekosistemah. (Chernivtsi, 2010). DrukArt, Chernivtsi, 37–39. [In Ukrainian with English summary]

Kutsokon Y, Kvach Y (2021) Invasive, neolimnetic and aboriginal fish species in Dnipro, Danube and Southern Buh basins (Ukraine, 2021). Version 1.7. Ukrainian Nature Conservation Group (NGO). Occurrence dataset accessed via GBIF.org on 2022-11-14. https://doi.org/10.15468/pwtyfq

Kutsokon Y, Roman A (2021) The own findings of fish of Ukraine during 2001–2021. Version 1.6. Ukrainian Nature Conservation Group (NGO). Occurrence dataset accessed via GBIF.org on 2022-11-14. https://doi.org/10.15468/zdqq8t

Kutsokon Y, Didenko O, Shcherbatiuk M, Gurbyk O, Buzevych O, Marushchak O (2021a) Fishes of water bodies of Rzhyshchiv city amalgamated territorial community (CATC). Version 1.5. Ukrainian Nature Conservation Group (NGO). Occurrence dataset accessed via GBIF.org on 2022-11-14. https://doi.org/10.15468/ftwx4e

Kutsokon Y, Roman A, Kvach Y, Shcherbatiuk M (2021b) Fish communities in three rivers of the South Podolia, Black Sea basin, Ukraine. Acta Zoologica Bulgarica 73(3): 385–391.

Kutsokon YK, Yuryshynets VI, Shcherbatiuk MM, Marushchak OY, Zaichenko NV, Dupak VS (2022) Alien fish species and their parasites of the Zdvyzh River: General characteristics, marker indicators, the monitoring scheme. Hydrobiological Journal 58(6): 28–45. https://doi.org/10.1615/HydrobJ.v58.i6.20

Kvach Y (2010) Helminths of the marbled goby (*Pomatoschistus marmoratus*), a Mediterranean immigrant in the Black Sea fauna. Vestnik Zoologii 44(6): 509–518. https://doi.org/10.2478/v10058-010-0034-6

Kvach Y, Kutsokon Y (2017) The non-indigenous fishes in the fauna of Ukraine: A potentia ad actum. BioInvasions Records 6(3): 269–279. https://doi.org/10.3391/bir.2017.6.3.13

Kvach Y, Ondračková M, Janáč M, Jurajda P (2016) Methodological issues affecting the study of fish parasites. I. Duration of live fish storage prior to dissection. Diseases of Aquatic Organisms 119(2): 107–115. https://doi.org/10.3354/dao02990

Kvach Y, Ondračková M, Bryjová A, Jurajda P (2017) Parasites as biological tags of divergence in Central European gudgeon populations (Actinopterygii: Cyprinidae: Gobioninae). Biologia 72(6): 671–679. https://doi.org/10.1515/biolog-2017-0073

Kvach Y, Kutsokon I, Roman A, Čeirāns A, Pupins M, Kirjušina M (2020) Parasite acquisition by the invasive Chinese sleeper (*Perccottus glenii* Dybowski, 1877) (Gobiiformes: Odontobutidae) in Latvia and Ukraine. Journal of Applied Ichthyology 36(6): 785–794. https://doi.org/10.1111/jai.14100

Kvach Y, Snigirov S, Leonchyk Y, Zamorov V (2022) The first data on parasite community of the black scorpionfish, *Scorpaena porcus* (Actinopterygii: Scorpaenidae), from the north-western Black Sea. Journal of Applied Ichthyology 38(2): 204–211. https://doi.org/10.1111/jai.14300

Leonardos I, Trilles J-P (2004) Reproduction of *Mothocya epimerica* (Crustacea: Isopoda: Cymothoidae), parasitic on the sand smelt *Atherina boyeri* (Osteichthyes: Atherinidae) in Greek lagoons. Diseases of Aquatic Organisms 62: 249–253. https://doi.org/10.3354/dao062249

Leppäkoski E, Gollasch S, Olenin S (2002) Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, 584 pp. https://doi.org/10.1007/978-94-015-9956-6

Lom J (1962) Trichodinid ciliates from fishes of the Rumanian Black Sea coast. Parasitology 52(1–2): 49–61. https://doi.org/10.1017/S0031182000023982

Lom J, Dyková I (1992) Protozoan parasites of fishes. Elsevier, New York, 315 pp.

Mackenzie K (2002) Parasites as biological tags in population studies of marine organisms: An update. Parasitology 124(7): 153–163. https://doi.org/10.1017/S0031182002001518

Malmberg G (1957) Om forekomsten av *Gyrodactylus* pa svenska fiskar. Skrifter Utgivna av Sodra Sveriges Fiskeriforening 1956: 19–76.

Marenkov ON (2018) Abundance and biomass estimation of this summer individuals of alien fish species in Zaporizke Reservoir. Ukrainian Journal of Ecology 8(1): 92–96. https://doi.org/10.15421/2018_192

Mierzejewska K, Kvach Y, Woźniak M, Kosowska A, Dziekońska-Rynko J (2012) Parasites of an Asian fish, the Chinese sleeper *Perccottus glenii*, in the Włocławek Reservoir on the Lower Vistula River, Poland: In search of the key species in the host expansion process. Comparative Parasitology 79(1): 23–29. https://doi.org/10.1654/4519.1

Moser M (1991) Parasites as biological tags. Parasitology Today 7(7): 182–185. https://doi.org/10.1016/0169-4758(91)90128-B

Movchan YV (2011) Ribi Ukraïni. [Fishes of Ukraine.] Zoloti Vorota, Kyiv, Ukraïna, 444 pp. [In Ukrainian]

Movchan YV (2012) Sučasnîj sklad îhtîofauni basejnu verhn'oho Dnipra (faunističnij oglâd). [Contemporary fish fauna of the Upper Dnipro basin (faunistic review).] Zbìrnik prac′ zoologìčnogo muzeû 43: 35–50. [In Ukrainian with English summary]

Movchan YV, Roman AM (2014) Sučasnîj sklad îhtîofauni basejnu seredn′oho Dnipra (faunističnij oglâd). [Modern fish fauna of middle Dnipro basin (faunistic review).] Zbìrnik prac′ zoologìčnogo muzeû 45: 25–45. [In Ukrainian with English summary]

Ondračková M, Slováčková I, Trichkova T, Polačik M, Jurajda P (2012a) Shoreline distribution and parasite infection of black-striped pipefish *Syngnathus abaster* Risso, 1827 in the lower River Danube. Journal of Applied Ichthyology 28(4): 590–596. https://doi.org/10.1111/j.1439-0426.2012.01967.x

Ondračková M, Šimková A, Civáňová K, Vyskočilová M, Jurajda P (2012b) Parasite diversity and microsatellite variability in native and introduced populations of four *Neogobius* species (Gobiidae). Parasitology 139(11): 1493–1505. https://doi.org/10.1017/S0031182012000844

Ondračková M, Kvach Y, Martens A, Jurajda P (2019) Limited parasite acquisition by non-native *Lepomis gibbosus* (Antinopterygii: Centrarchidae) in two ponds at the Upper Rhine in Germany. Journal of Helminthology 93(4): 453–460. https://doi.org/10.1017/S0022149X18000469

Ondračková M, Janáč M, Borcherding J, Grabowska J, Bartáková V, Jurajda P (2021) Non-native gobies share predominantly immature parasites with local fish hosts. Journal of Vertebrate Biology 70(4): 21050. https://doi.org/10.25225/jvb.21050

Öztürk T, Güven A (2022) Trichodinid ectoparasites (Ciliophora: Peritrichida) from gills of some marine fishes of Sinop coasts of the Black Sea, with the first report of *Trichodina rectuncinata*. Aquatic Research 5(4): 295–306. https://doi.org/10.3153/AR22029

Panov VE, Alexandrov B, Arbačiauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RSEW, Nehring S, Paunović M, Semenchenko V, Son MO (2009) Assessing the risks of aquatic species invasions via European inland waterways: From concepts to environmental indicators. Integrated Environmental Assessment and Management 5(1): 110–126. https://doi.org/10.1897/IEAM_2008-034.1

Polačik M, Janáč M, Trichkova T, Vassilev M, Keckeis H, Jurajda P (2008) The distribution and abundance of the *Neogobius* fishes in their native range (Bulgaria) with notes on the non-native range in the Danube River. Fundamental and Applied Limnology 18(Suppl. 166): 193–208. https://doi.org/10.1127/lr/18/2008/193

Poulin R, Kamiya T (2015) Parasites as biological tags of fish stocks: A meta-analysis of their discriminatory power. Parasitology 142(1): 145–155. https://doi.org/10.1017/S0031182013001534

Sekulić N, Cakić P, Lenhardt M, Vučić D, Budakov LJ (1999) Short-snouted pipefish *Syngnathus abaster* (Acanthopterygii: Syngnathidae) in Yugoslav section of the Danube. Ichthyologia 3: 79–82.

Semenchenko V, Son MO, Novitski R, Kvach Y, Panov VE (2016) Checklist of non-native benthic macroinvertebrates and fish in the Dnieper River basin. BioInvasions Records 5(3): 185–187. https://doi.org/10.3391/bir.2016.5.3.10

Sharpilo VP, Monchenko VI (1971) On the life cycle of *Ophiotaenia europaea* Odening, 1963 (Cestoda, Ophiotaeniidae). Vestnik Zoologii 6: 90–92.

Slastenenko E (1956) Karadeniz havzası balıkları. E.B.K. Yayini, Istanbul, 711 pp.

Snigirov SM, Zamorov VV, Karavanskyi YV, Pitsyk VZ, Kurakin OP, Abakumov OM, Liumkis PV, Snigirov PM, Morozov YV, Kvach YV, Kutsokon YK (2020) Taksonomîčna ta ekologo-faunîstichna harakteristika sučasnoï îkhtîofauni Odeskoï zatoki, Dnîstrovskogo peredgirlovogo uzmorâ î priberežnih vod o. Zmîînyj. Visnyk Odeskoho natsionalnoho universytetu. Biolohiia 25(2): 113–139. https://doi.org/10.18524/2077-1746.2020.2(47).218060 [In Ukrainian with English summary]

Sørensen TA (1948) A new method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of vegetation on Danish commons. Kongelige Danske Videnskabernes Selskabs, Biologiske Skrifter 5: 1–34.

Sreedevi C, Prasuna K, Lavanya K, Kanaka Swarna Latha K (2017) *Contracaecum rudolphii* Hartwich, 1964 (Nematoda: Anisakidae) in a wild spot-billed pelican (*Pelecanus philippensis*): a case report. Journal of Parasitic Diseases 41(4): 959–962. https://doi.org/10.1007/s12639-017-0918-2

Tutman P, Burić M, Skaramuca B (2012) First substantiated record of the black-striped pipefish, *Syngnathus abaster* (Actinopterygii: Syngnathiformes: Syngnathidae), in the freshwaters of Bosnia and Herzegovina. Acta Ichthyologica et Piscatoria 42(3): 259–262. https://doi.org/10.3750/AIP2011.42.3.11

WoRMS (2022) World Register of Marine Species. [Accessed 2022-10-27.] https://doi.org/10.14284/170

Xu K, Song W, Warren A, Choi JK (2001) Trichodinid ectoparasites (Ciliophora: Peritrichida) of some marine fishes from coastal regions of the Yellow Sea and Bohai Sea. Systematic Parasitology 50(1): 69–79. https://doi.org/10.1023/A:1011865124047

Yurishinets VI (2010) Symbiotic organisms of some alien species of freshwater fishes and mollusks of water bodies of the Danube River and Dnieper River basins. Russian Journal of Biological Invasions 1(2): 141–144. https://doi.org/10.1134/S207511171002013X

Zaitsev YP (1992) Ekologičeskoe sostojanie šelfovoj zony Černogo morâ u poberež'â Ukrainy (obzor). Gidrobiologičeskij žurnal 28(4): 3–18. [In Russian with English summary]

Zimbalevskaya LN, Sukhoivan PG, Chernogorenko MI (1989) Bespozvonočnye i ryby Dnepra i jego vodohranilišč. Naukova Dumka, Kiev, USSR, 242 pp. [In Russian]